SOME HOURLY OBSERVATIONS OF TREE GROWTH

AUGUST P. BEILMANN

Manager, Missouri Botanical Garden Arboretum

Although everyone has observed the active response of trees to the seasons, yet trees are often thought of as static organisms,—capable, it is true, of performing certain functions in certain seasons or even remaining quiescent during the cold of winter but without the capacity of immediate adjustment to slight changes in environment. The habit of producing leaves in spring is generally associated with the increasingly warmer and brighter sunshine of that period. Likewise, the unfolding of flowers, the development of fruit, and the autumnal coloration are dependent upon seasonal changes in weather. These reactions are annually observed and appreciated. It is not generally known, however, that the duration of sunshine for any one day may require a profound adjustment on the part of the tree.

Numerous investigations have been made on the effect of environmental conditions upon tree growth. The literature contains many references to the response of trees to one or more meteorological phenomena. However, all the factors which have an effect upon the growth rate have not been studied simultaneously, nor have continuous and automatic records of them been made.

This study was undertaken to determine, if possible, the effect of weather upon the physiological processes of a tree. Since most physiological activity is finally manifested as growth, it was believed that a continuous record of growth—known to be of seasonal occurrence—might be correlated with the prevalence of certain external factors exhibiting similar periodicity. Thus, the conditions peculiar to early spring (abundant moisture, low temperature, short days, etc.) might show a correlation with the beginning of growth, or with its gradual decline upon the approach of summer. After the growth peak had passed other conditions would prevail (those of late summer, for instance, with longer days, less moisture and higher temperatures); and again a continuous record might show certain physiological relationships which in turn would differ from those of winter. Thus if the entire range of temperatures, seasonal amounts of sunshine and of precipitation are checked against the carefully recorded responses of the tree, certain individual and combined influences of these environmental factors might be reflected in its growth. The work herein outlined is intended as a preliminary report. Since identical weather conditions are of infrequent occurrence, many of the recorded relationships of these factors to tree growth have not been repeated, and the following discussion is based largely upon extreme conditions.

A critical study of tree growth must take into consideration both the systems of photosynthesis and translocation peculiar to trees. While this study does not specifically touch upon either system, the interpretation of the accumulated data might have a bearing upon these problems. Since Curtis[1] has exhaustively discussed the literature and indicated the present status of the work while Gibbs[2] has cited an additional several hundred papers, no further bibliographical references will be made in the discussion to follow.

For this study a Bur Oak (*Quercus macrocarpa* Michx.) 34 years old was selected. This tree grew near the center of a small group of mixed White and Black Oaks and had received little pruning. The growth rate had been normal and as it had never been suppressed the tree developed a low wide-branched crown with a trunk 30 inches in diameter, 1 meter above ground level. Every effort was made to permit the tree to grow independent of any artificial stimulus, and throughout the period of observation it received no pruning, spraying, fertilizing or irrigation. This report covers a period of 70 weeks, from July 16, 1933, to November 25, 1934.

METHODS

During this investigation the dendrograph record was used as a basis for evaluating the effects of all the environmental factors. All external conditions which appeared to exercise some influence upon the growth of a tree were charted. Thus a continuous and automatic record was made of the air temperature, relative humidity, hourly wind movement, barometric pressure, precipitation, sunshine and soil temperature. Simultaneously, identical graphs were made of the expansion and contraction of the trunk by the use of the dendrograph, while the internal temperature and internal pressure were recorded automatically.

Since most of the instruments must of necessity be placed close to the tree under observation, a rectangular concrete block weighing approximately .95 kg. was cast within .3 dm. of the trunk to serve as a table. A shed 3 m. long, 1.3 m. wide and the same in height was built to enclose both the lower portion of the tree trunk and the concrete table. This shed was fitted with two large ventilators, one in the roof and another in the west side. The east side opened into a door, and the side walls extended to within 2 dm. of the ground level. This type of construction provided safety and shelter for the instruments during inclement weather, and at the same time allowed ample ventilation for accurate records. The sun record was taken on a roof several hundred meters from the tree. The barometer was located in a building approximately the same distance away. The hourly wind movement and precipitation records are from the St. Louis Office of the Weather Bureau, located about 7 km. from the tree. All other instruments were placed in the house built about the tree.

DENDROGRAPH

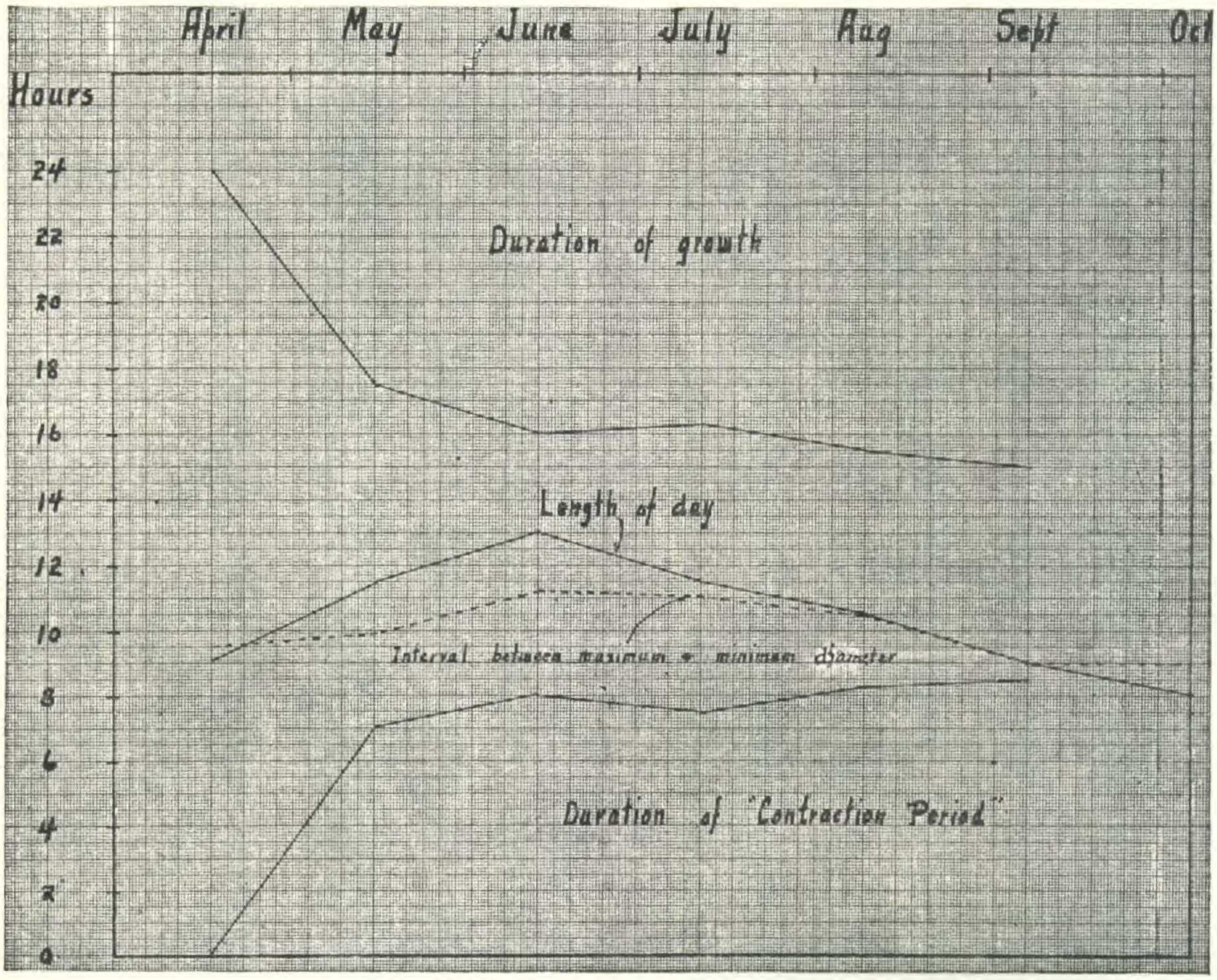
This instrument was developed by MacDougal[3], who has also carefully de-

[1] Curtis, O. F. The translocation of solutes in plants, New York, 1935.

[2] Gibbs, R. D. Studies in tree physiology I. Can. Jour. Res C **17**:460-482. 1939; II. C **18**:1-9. 1940; III. C **20**:236-240. 1942.

[3] MacDougal, D. T., J. B. Overton, and G. M. Smith. The hydrostatic-pneumatic system of certain trees: movements of liquids and gases. Carnegie Inst. Washington Publ. 397. Washington, 1929.

scribed it and calculated its accuracy. It is capable of providing a continuous and accurate record of all tree-trunk fluctuations. Changes in diameter of a tree trunk being essentially manifestations of growth, the dendrograph becomes the most important instrument in a study of growth and the factors affecting it. For this study it was attached in the usual manner. The contact points touched a smoothed portion of the trunk, on opposite sides, about one meter above the ground. Since the contact rods touched the newer layers of the phloem the record is essentially a measurement of the actively growing portion of the tree. What influence external conditions have upon the xylem alone cannot be determined from this record.



Relation of daylight to tree growth.

In spring, about ten days after the initial swelling of the buds but before they reach 1½ inches in length, the dendrograph shows a marked daily rhythm in expansion and contraction. The peak of the expansion is reached between 4 A. M. and 6 A. M. At exactly 6 A. M.—on sunny normal days—the trunk begins to contract, reaching its smallest diameter for the 24-hour period at 4 P. M. From then no change occurs until exactly 6 P. M., when the expansion begins and continues until the following morning at 6 o'clock. This rhythm is constant on clear days when the tree is in leaf. However, during rain—no matter how slight

—and on cloudy or humid days the rhythm is temporarily interrupted. At such times the tree fails to contract in the period from 6 A. M. to 4 P. M. Should only a part of the forenoon be cloudy and the rest with full sun, contraction may begin later and last only a short time. Even the normal expansion, which begins at 6 P. M., may be delayed until midnight or after and it may continue until noon of the next day. This variation of the normal rhythm is only temporary, however, and the first cloudless day usually establishes the daily expansion and contraction. The degree of expansion and contraction and the length of the quiescent period, after attaining either the maxima or minima, are dependent entirely upon the sunshine and the relative humidity. Thus a cloudy day in midsummer shortens the contraction period as much as three hours; the minimum may be reached at 1 P. M. During that same morning the contraction period may have been delayed two hours; or until 10 A. M. Since the dendrograph record indicates that a certain amount of the daily expansion is dependent upon water absorption, the contraction must be the result of water loss. In this manner, the daily growth is obscured except as it shows in the slowly rising peaks of the dendrograph record.

All growth in diameter occurred between April 10 and June 7, a period of ten weeks. No growth is evident in the record after June 7, although this is the period during which the "summer wood" is usually expanded. The fact that during cloudy humid weather, in the absence of any notable contraction, there still exists a rhythmic increase in diameter, seems to indicate that whatever growth occurs is accomplished after midnight, the period during which this increase is normal. If the rhythmic diameter changes are accepted as indications of water loss or absorption, then the dendrograph clearly shows how minute is the lag between utilization and replenishment. The dendrograph reflects the condition of the cells adjacent to the point of contact on the trunk, in this case a halfway point between utilization of the water by the leaves and replenishment which is the function of the roots. Therefore, the rhythmic contraction beginning at 6 A. M., when only the top of the tree is exposed to the full morning sun, indicates that the effect of evaporation from that part is almost instantly felt throughout the tree. The rhythmic diameter changes occur throughout both the growing and the summer periods. Approximately two weeks previous to the shedding of the leaves the dendrograph record becomes a straight line and remains so except for minor fluctuations correlated with the internal temperature. At this time the cooling effect of actively transpiring leaves gradually diminishes, and the internal temperature gradually rises until the typical dormant record is produced. This is unmodified by transpiration and fluctuates as widely as the air temperature. Thus a close study of both the dendrograph and the internal temperature records will reveal the approximate hour during which the formation of the abscission layer begins. It will also show the time required for this formtion to affect all the leaves, thereby designating the hour of dormancy. The reversal of this process—the change back to rhythmic fluctuations—will, during the following spring, designate the hour of awakened physiological activity.

During extremely cold weather, when the internal temperature is finally lowered to —7° C., the tree immediately contracts and remains contracted until the temperature again rises. The contraction during times of extreme cold is in a straight-line relationship to the internal temperature. After the initial sharp contraction at —7° C., the diameter of a tree varies exactly as the internal temperature varies.

INTERNAL TEMPERATURE

To obtain this record a soil-thermograph was inserted in a 20-mm. hole bored through the trunk to within 80 mm. of the opposite side. Afterward a plug of asbestos was rammed in, leaving only the flexible tube extending. The entire opening was then sealed over with an asphaltic compound.

During the dormant period the record taken by this instrument is simply a smoothed curve of the air temperature, exhibiting whatever lag the insulating efficiency of the tree trunk imparts. Usually the internal temperature remains about 8° F. lower than the maximum summer air temperature, but it never exceeds 86° F. so long as the tree is supplied with some soil moisture. During the winter the internal temperature remains about 5° higher than the minimum. There are, however, rhythmic variations of internal temperature which are correlated with periods of stormy and fair weather, as well as distinctive seasonal trends. During the period of growth and its cocomitant transpiration the record is closely linked with that of the dendrograph, the internal temperature being highest at the peak of expansion and coolest when the contraction is greatest. Incidentally, the peak of expansion and also of internal temperature occurs during the early morning hours, coincident with the lowest air temperature and the lowest evaporativity of the air for the previous 24 hours. There is a marked tendency toward higher internal temperatures, sometimes an immediate increase, following a rain during the growing period. Should either the precipitation or the accompanying cloudy weather last for 24 hours, the internal temperature slowly declines to a point well below the daily minimum. The initial rise is traceable to the lessened transpiration during the actual rainy period. The decrease below the daily low record seemingly is the result of the accelerated transpiration, since following a rain more water is available. After the initial rise the periodicity of the rhythm is reversed, the internal temperature varying inversely with the dendrograph until the stormy period has passed. The cool morning hours find the tree coolest. This would not be true when the air temperature dropped considerably after rains, for then the lowered air temperature, no doubt, is chiefly responsible. However, if evaporativity is closely related to air temperature a rise in internal temperature should follow such cool periods, since there would be less water loss from transpiration. In any event the individual effects of these phenomena cannot be separated, and in all probability both become operable under certain conditions and may mask their interlocking effects.

SOIL TEMPERATURE

The recording element of a soil-thermograph was placed 22 inches below the surface under the branch tips. This position was chosen after explorations showed the presence of a large number of "feeding" roots in this area. The soil surface around the tree and extending beyond the branch spread was without vegetation. During the summer the portion above the thermograph element received sun for only 1½ hours during the mid-day.

The record of the soil temperature discloses no great daily range, and the annual record appears as a smoothed curve of the internal temperature. In the absence of marked daily or weekly fluctuations, the effects of soil temperature could not be traced on the dendrograph. Thus, although this factor does not have an hourly effect upon the tree it probably does influence the seasonal occurrence of growth. In this connection it is interesting to note that all spring growth in diameter occurred within the comparatively narrow limits of 15° F. Growth began in April coincident with a soil temperature of 50° F. and ceased the first week of June with a soil temperature of 65° F. A maximum of 78° F. was reached in July; the minimum, 29° F., during the first week of March. Comparative figures of soil temperatures from more exposed situations are not available, but it is certain that they were higher during the dry spring and very dry hot summer. Whether the heat reacted unfavorably upon the trees is not known. The temperature recorded under the tree observed was probably not inhibitory to growth; insufficient water seems more likely to have been the limiting factor in the period after June.

PRECIPITATION

This record, as well as the wind record, was taken from the St. Louis Office of the Weather Bureau, a distance of about 7 km. from the tree. During most of the year duration of rain at the two stations is practically the same, and the total precipitation does not usually vary greatly. However, during the hot dry months of June, July and August, weather conditions may be altogether different at the two stations. It is during these hot dry spells that the effect of precipitation is most easily determined, and for that season the record is simply an observation.

Certain periods of the dormant season are generally considered as devoted to water storage. However, the effects of rain were noted only during the summer, when even slight amounts (.01 inch) were recorded by an upward rise in the dendrograph. The abruptness of the rise and its continuance depended entirely upon the total rainfall. Precipitation of only .01 inch was beneficial chiefly because of the humid conditions prevailing at the time. Much more rain was necessary to percolate sufficiently to reach the roots. The reaction to larger amounts of rain, which in 1933 and 1934 occurred only in very early spring, are not easily discernible. In spring, the tree is usually well supplied with moisture, since transpiration has not reached the peak of midsummer and temperatures are uniformly lower. Therefore, slight fluctuations in both the dendrograph and the records of internal temperature cannot be interpreted as resulting solely from rain. It is hoped that future less droughty years will yield a record showing the effect of substantial rains in midsummer. During the fall of both 1933 and 1934 there was an abrupt increase in tree diameter coincident with the beginning of the seasonal rains. That this increase was not maintained may have been due to the extremely dry weather characteristic of the winter following. Other more favorable seasons might show the late September increase coincident with the fall rains to be of a permanent character. The absence of any marked diameter increase after rainfall, in either fall, winter or early spring is difficult to account for, since both water loss and gain, as well as growth, are charted in the dendrograph record and can be easily separated.

RELATIVE HUMIDITY

A continuous humidity record was obtained from a hygro-thermograph placed on the concrete block in the shelter previously described.

Throughout both the "growing" and the "summer" seasons, during clear weather, the humidity is highest between midnight and 4 A. M. Then it begins to decline and reaches the lowest point about noon. Changes in relative humidity affect the evaporating power of the air and consequently alter the transpiration rate, as is clearly shown in the dendrograph record. Both the humidity record and the dendrograph record show a peak in the early morning hours. The humidity declines first, and shortly after the dendrograph records a contraction of the trunk. Since the relationship between tree diameter and humidity is so close any factor capable of modifying the humidity will affect the tree sufficiently to be incorporated in the dendrograph record. On cloudy days, which are usually accompanied by higher and more nearly uniform humidity, the tree undergoes only a limited contraction. The more uniform dendrograph record continues as long as the humidity remains above that of normal bright days. During the cooler portions of late summer, the dendrograph shows a delay in the beginning of the contraction period coincident with the presence of dew. While the almost instantaneous responses of the tree to changes in relative humidity have been demonstrated, the fact remains that the daily period of contraction begins at 6 A. M. regardless of the average monthly humidity readings, which tend to decrease from April to July and to increase toward October. Thus the average monthly humidity readings for 1943 show:

	7 A. M.	7 P. M.
April	64%	57%
May	59%	43%
June	66%	49%
July	61%	42%
August	73%	59%
September	86%	72%
October	74%	54%

Since humidities do not tend to be lower in midsummer than during other growing seasons, seasonal shifting of contraction and expansion periods following the daylight hours is not reflected in the humidity reading. Essentially, humidity changes affect the tree instantaneously and therefore show no seasonal rhythm.

WIND MOVEMENT AND AIR TEMPERATURE

These two factors show no seasonal trend. The wind movement remains nearly constant throughout most of the growing season. Its effect upon the tree is immediate, and we have observed a very rapid rise or fall in internal temperature due to accelerated wind movement prior to a thunderstorm. The air temperature gradually rises to a peak in summer and then declines. Apparently it has only a limited effect upon the tree, since any rise or fall in air temperature is usually correlated with certain very definite weather changes, and it would be reflected in other records.

BAROMETRIC AND INTERNAL PRESSURE

Certain of the hourly charts indicate an interesting relationship between barometric pressure and the behavior of the tree. However, the precise effect of a rising or falling barometer must be left to a subsequent study more concerned with a shorter time interval than used in this study. The internal pressure, an extraordinarily interesting measurement of the activity of a tree, has been reported upon.[4] These two factors are again without seasonal trend, and since their effect upon the tree is instantaneous, the records obtained must be read to a very short time interval, perhaps 5 minutes or less.

SUNSHINE

The length of day, changing as it does from season to season, might be expected to exert a profound influence on the behavior of a tree. That it does is apparent from the dendrograph record and also from the internal temperature. In April the interval in the daylight hours between maximum and minimum diameter is only 9 hours, in May it is 9.9 hours, and in June, with 13 hours of sunshine, it increased to 11.3 hours. This means that as the sun rises earlier toward the latter part of June the tree begins to shrink early in the morning and reaches and maintains its small diameter later in the day. During this early period, when active growth is taking place, the effect of sunshine is very marked, although the contraction or expansion of the trunk is not as closely tied to length of day as it is through the months of August and September. During the late fall contraction begins with sunrise, and expansion begins with sunset. It is known, however, that in addition to seasonal trends sunshine does cause an immediate change in the activity of a tree. Some evidence exists to show that the passing of each cloud on an otherwise clear day modifies the functions of the tree to the extent that they can be recorded. Thus the dendrograph and the internal temperature readings both leave a record indicating the passing of a cloud. The immediate effect of

[4] Beilmann, August P. An attempt to record internal tree-trunk pressures. Ann. Mo. Bot. Gard. **27**:365-370.

sunshine on a tree will be the subject of later investigation. As a general thing, a bright sunny day accelerates transpiration, depresses the internal temperature, and initiates the beginning of the contraction period.

SUMMARY

Several thousand weekly charts have been obtained from a series of automatic recording instruments. These show some interrelationship between "weather" at a particular hour and some modifications to it on the part of the tree, depending upon whether or not the external factor favored or inhibited growth.

The dendrograph has proven of value in recording seasonal trends but some modification of the instrument is required for a critical study of tree behavior.

The internal temperature shows a seasonal trend but is equally important for a short-time study. It is rather difficult, however, to localize the reading and in this study the average of the trunk diameter was obtained.

The soil temperature is a seasonal factor playing a role at the beginning and perhaps at the end of the growing season.

Precipitation, as might be expected, is seasonal and exhibits a pronounced effect very quickly when it occurs out of season. A calculation from October to October probably gives a clearer picture of the moisture need and utilization of the tree than does a record based on the calendar year. During a very dry portion of the year the tree immediately reacts to any form of moisture whether rain, dew, or high humidity.

The hourly wind movement and the maximum wind velocity are without seasonal effects. Wind cannot be dismissed, however, since observation has shown a striking relationship between velocity and internal temperature.

The air temperature varies with the season, and does not show either marked seasonal trends or rapid effects, largely because all other factors are changing just as rapidly. For instance, since a very sharp rising or falling temperature may be accompanied by rain, on the one hand, and a dry period, on the other, the effects are lost in the other records.

The barometric pressure and the internal pressure might be expected to yield some interesting records. However, the effects seem to be lost in any seasonal study of behavior. They may be investigated in a study dealing with a short-time interval.